BROWN SHRIMP ON THE EDGE: LINKING HABITAT TO SURVIVAL USING AN INDIVIDUAL-BASED SIMULATION MODEL

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Abstract. In many coastal areas, natural habitats are being fragmented and lost to encroaching human development. These landscape changes can affect the production of recreationally and commercially important fisheries because many exploited species of fish and shellfish are estuarine dependent and utilize coastal marshes as nursery grounds. Brown shrimp are an example of a commercially exploited species that may be highly affected by changes in the spatial distribution of habitat types. We used a spatially explicit, individual-based simulation model to explore the role of marsh vegetation and edge habitat in brown shrimp survival. The model simulated shrimp movement, mortality, and growth of individual shrimp from arrival as postlarvae to 70-mm body length, when they emigrate offshore. Simulations were performed on 100×100 m spatial grid of 1-m^2 cells, with each cell labeled as ''water'' or ''vegetation''. Predation mortality was influenced by shrimp size, movement, and habitat. Simulated shrimp growth depended on temperature, habitat, and local shrimp density. We examined the relationships between shrimp survival and marsh attributes (amount of vegetation and edge habitat) by simulating a series of four habitat maps that we created from aerial photographs. Biological parameters were derived from published estimates and from field data. We corroborated the model by comparing the simulated shrimp abundance with summary statistics from long-term monitoring data, by comparing the simulated density with fine-scale patterns observed in field studies, and by comparing simulated and measured stable-isotope values. Surviving shrimp grew faster, moved less, spent more time in vegetation, and experienced slightly higher local densities than shrimp that died during the simulation. Habitat maps with more edge habitat invariably produced higher simulated shrimp survival rates. High-edge habitats increased survival by providing shrimp more direct access to vegetation without additional movement-related mortality and density-dependent growth costs associated with low-edge habitats. Model predictions were robust to higher numbers of initial postlarvae and to alterations to the movement rules. The results of this study suggest that the management of brown shrimp should be extended from protecting the spawning stock through catch regulations to also protecting the estuarine life stages through habitat conservation and restoration.

Key words: brown shrimp; Gulf of Mexico (USA) fisheries; habitat fragmentation; habitat loss; marsh-edge habitat, management; model, individual-based; simulation model; stable isotopes.

INTRODUCTION

Estuaries are important to the production of recreationally and commercially important fisheries. Many exploited species of fish and shellfish are estuarine dependent and utilize coastal marshes as nursery grounds. For example, the juvenile stages of shrimp, stone crabs, red drum, gray snapper, and bluefish inhabit estuaries in the northern Gulf of Mexico (Minello 1999). Salt marsh vegetation is common in many estuaries and often supports elevated densities of nekton compared to nonvegetated habitat types (Zimmerman et al. 1984, Rozas and Minello 1998, Rozas and Zimmerman 2000). Juveniles may congregate in vegetated areas of estuaries because of abundant food supplies or for refuge from predation (Boesch and Turner 1984).

In many coastal areas, natural habitats are disappearing or becoming fragmented. Causes of wetland fragmentation include both anthropogenic and natural factors: encroaching human development, elimination of riverine inputs, sea-level rise, and natural deltaic processes such as subsidence (Boesch et al. 1984). The highest coastal land-loss rates in the United States oc-
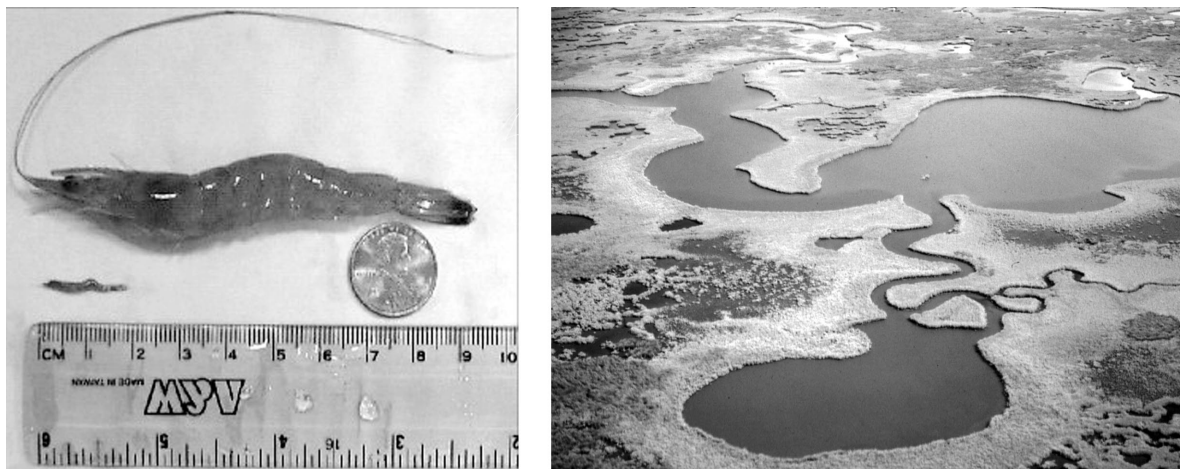
PLATE 1. (Left) Size comparison between a young brown shrimp that would be coming into the estuary and a subadult leaving the estuary, 15 mm vs. 95 mm total length. A penny and a ruler are shown for reference. Brown shrimp biomass increases dramatically in marsh nursery areas. Photo credit: Brian Fry and Mark Benfield. (Right) Aerial photograph of marsh landscape in coastal Terrebonne Parish, Louisiana, USA. Photo credit: Lawrence Rozas.

cur in Louisiana (Barras et al. 1994), which supports the largest commercial fishery harvest (biomass and exvessel dollar value to the harvester) in the continental United States (O'Bannon 2002). Fragmentation and land loss in the Mississippi River delta region will continue to result in dramatic changes in the pattern of coastal habitats. Understanding the spatial component of ecological processes, such as how marsh arrangement affects growth and survival, is an essential component of managing estuarine-dependent fish and shellfish species.

Brown shrimp *Farfantepenaeus aztecus* (formerly *Penaeus aztecus*; see Perez-Farfante and Kensley 1997) is an example of a commercially exploited species that may be highly affected by changes in the spatial distribution of marsh habitat (see Plate 1). Like other estuarine-dependent species, adult brown shrimp spawn offshore; the larvae move shoreward; and postlarvae settle in the estuaries. Juveniles grow within the estuary and then migrate offshore. Juvenile survival within the estuary is important to examine because the year-class strength of brown shrimp is likely established between postlarval entrance to the estuary and migration offshore (Barrett and Ralph 1977, Minello et al. 1989, Haas et al. 2001).

Shrimp production appears to be influenced by physical marsh attributes (Zimmerman et al. 2000). On a system-to-system basis, more extensive wetland systems produce higher shrimp harvests (Turner 1977, 1992). The amount of edge habitat is important because juvenile brown shrimp are found associated with vegetation within a few meters of the vegetation–water interface (Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000). As marshes disintegrate, the amount of edge habitat follows a dome-shaped curve, initially increasing, then peaking at intermediate

levels of disintegration, and finally decreasing at high levels of disintegration (Browder et al. 1985). Given the high rate of coastal wetland loss in Louisiana (Britsch and Dunbar 1993) and the dome-shaped relationship between edge habitat and marsh disintegration, it is critical to examine the relationship between vegetated edge habitat and brown shrimp survival.

In this study we developed a fine-scale, spatially explicit, individual-based simulation model to explore the relationships among vegetation, vegetated edge habitat, and brown shrimp survival. The model tracked the movement, mortality, and growth of individual shrimp during their residence in estuarine marshes. The relationship between shrimp survival and marsh attributes (amount of vegetation and vegetated edge habitat) were examined by overlaying the simulation model on various habitat maps that we created from aerial photographs. We examined simulated shrimp survival across four habitat maps that had different amounts of vegetation and edge habitat. Our overarching hypotheses are that more vegetation and more edge habitat will enhance shrimp survival, and that individuals that survive will have characteristics (e.g., habitat usage, growth rate) distinguishable from those that die. The characteristics of surviving shrimp offer evidence of the underlying causes of the survival patterns documented in previous descriptive and correlative studies. We conclude by discussing the management implications of our results.

MODEL DESCRIPTION

The model simulated the biology and behavior of brown shrimp in a realistic marsh environment (Fig. 1). Each simulation lasted 245 days, beginning on 1 January and ending on 1 September. Individual shrimp were tracked on a 6-h time step and a 100 × 100 m
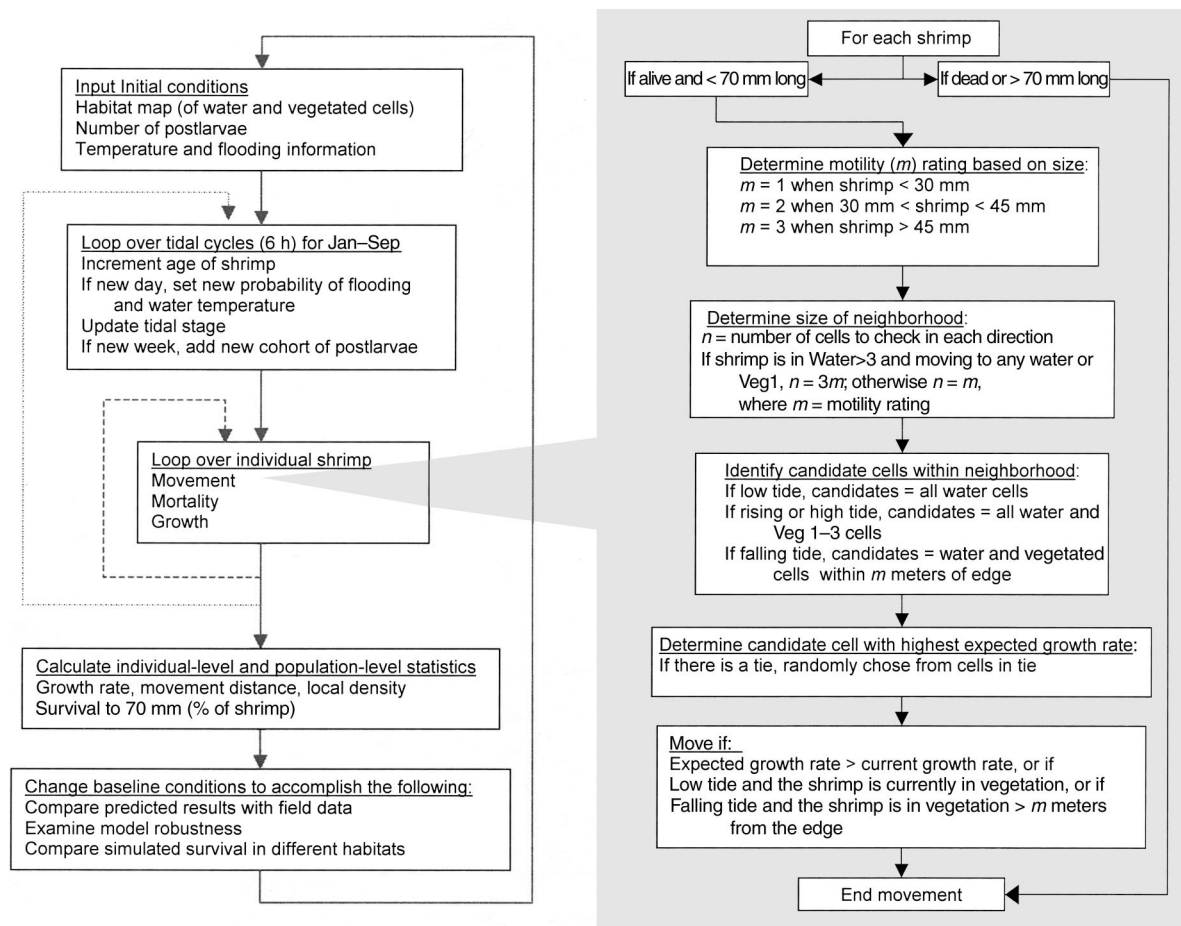
FIG. 1. Flow chart showing the major components of the simulation model, with additional detail provided about shrimp movement.

grid of cells (habitat map) from arrival as postlarvae to reaching 70 mm in body length. Each cell was labeled as "open water" or "vegetation". Water temperature was uniform on the grid and varied daily; temperature affected shrimp growth rate. The tidal stage of each cell was updated every 6-h. Flooded conditions provided shrimp with access to more cells. Model predictions included characteristics of individual shrimp (e.g., percentage of time in vegetated cells) and population-level statistics (e.g., percent survival to 70 mm).

Specification of the physical environment

The physical environment in the model was composed of a habitat map (100×100 m grid of water and vegetated cells), water temperature, and tidal inundation of marsh vegetation. Habitat, temperature, and marsh inundation were included because they are historically correlated with shrimp behavior and survival (Barrett and Gillespie 1973, Turner 1977, Browder et al. 1989, Childers et al. 1990, Zimmerman et al. 1991). Other physical variables (such as salinity) were not included in this model because we considered them

less influential given the small spatial extent of the model.

Habitat maps.—We created four habitat maps with different amounts of vegetation and edge habitat. The habitat maps represented realistic marshscapes in southern Louisiana (USA) and were created by performing a vegetation–water classification on portions of the Cocodrie NE Digital Orthophoto Quarter Quadrangle (DOQQ) from a GIS digital map of Louisiana (version 2.0; available online).[7] A DOQQ is an orthorectified digital image of an aerial photograph. Each unit (or pixel) in the image represents one square meter and corresponds to a single cell on the habitat map. To create the habitat maps, we chose four 100×100 m subsets from the DOQQ and classified each square meter as water or vegetation (Fig. 2).

The four habitat maps were categorized based on their percentage of edge and vegetation. Table 1 describes the subclassification of water and vegetation cells. Cells at the edges of the habitats maps were classified by considering the map a continuous unit that
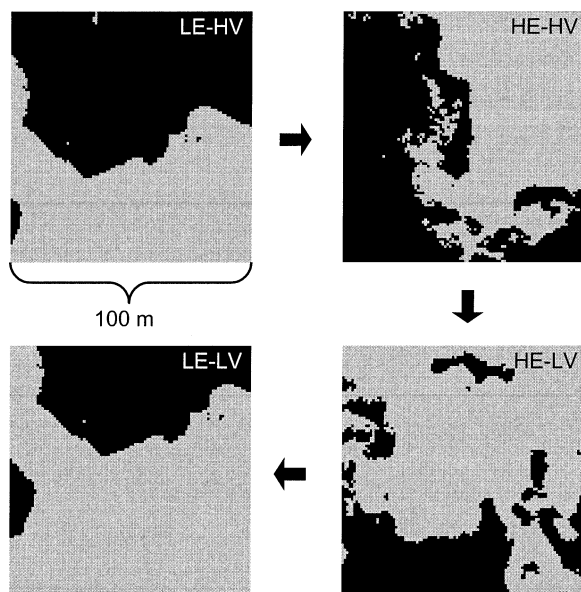
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[7] ⟨http://atlas.lsu.edu⟩

FIG. 2. The four 100×100 m habitat maps used in model simulations. The maps were created by subsetting and classifying portions of the Cocodrie NE Digital Orthophoto Quadrangle (DOQQ). The gray is water, and the black is vegetation. The four maps represent snapshots in a simplified continuum of marsh disintegration:
(a) LE-HV = little edge and high amount of vegetation;
(b) HE-HV = high edge and high amount of vegetation;
(c) HE-LV = high edge and low amount of vegetation;
(d) LE-LV = little edge and low amount of vegetation.

TABLE 1. Percentage of habitat types in each of the four habitat maps.

	Habitat maps			
Cells	LE–HV (%)	HE–HV (%)	HE–LV (%)	LE–LV (%)
Water, all cells	49.93	50.23	69.96	69.83
Water1	2.52	7.68	8.47	2.64
Water2	1.80	3.26	5.61	1.94
Water3	1.73	2.49	5.01	1.82
Water>3	43.88	36.80	50.87	63.43
Vegetation, all cells	50.07	49.77	30.04	30.17
Veg1	2.42	8.88	7.75	2.42
Veg2	1.70	4.76	3.90	1.65
Veg3	1.67	3.82	2.55	1.60
Veg>3	44.28	32.31	15.84	24.50

Notes: Maps represented habitats with low edge (LE), high edge (HE), low vegetation : water ratios (LV), and high vegetation : water ratios (HV). Water1, Water2, Water3, and Water>3 represented water cells that were within 1 m, 2 m, and 3 m of and >3 m from vegetation, respectively. Veg1, Veg2, Veg3, and Veg>3 represented vegetated cells within 1 m, 2 m, and 3 m of and >3 m from water, respectively.

wrapped around from top to bottom and from side to side. We use the term ''marsh'' to refer to the entire grid of cells on a habitat map. ''Edge'' and ''edge habitat'' refer to cells that border the interface between the vegetation and water (Veg1 and Water1 cells), with Veg1 cells called ''vegetated edge'' and Water1 cells called ''water edge.'' The differences among the four habitat maps were characterized by the percentage of the cells that were vegetated and by the percentage of cells that were vegetated edge.

Water temperature.—Water temperature varied daily and was uniform over each habitat map. Daily water temperatures were derived from measurements recorded by the Louisiana Department of Wildlife and Fisheries (LDWF) during 1970–1997 in Louisiana coastal marshes. Water temperature (TEMP, in degrees Celsius) was regressed against a trigonometric function of calendar day ($R^2 = 0.68$; Fig. 3):

$$\text{TEMP} = 23.157 - [2.459 \times \sin(\text{DAY} \times 0.017)]$$
$$- [7.161 \times \cos(\text{DAY} \times 0.017)] \qquad (1)$$

where DAY is the calendar day of the year.

Marsh inundation.—We simulated the tidal stages based upon observed inundation patterns in Louisiana marshes because access to vegetation within coastal Louisiana marshes is often driven by regularly occurring, seasonal meteorological events rather than astro-

nomical tides (Rozas 1995). We simulated a daily probability of flooding (P_f) by fitting a curve (Fig. 4a) to the estimated marsh inundation in a hummocky southern Louisiana *Spartina* marsh measured over a five-year period (Rozas and Reed 1993):

$$P_f = [30.885 - 0.673(\text{DAY}) + 0.0216(\text{DAY})^2$$
$$- 1.55 \times 10^{-4}(\text{DAY})^3$$
$$+ 3.36 \times 10^{-7}(\text{DAY})^4]/100. \qquad (2)$$

The tidal stage (i.e., rising, high, falling, or low) was updated every 6 h based on the probability of flooding and on the previous tidal stage. At the beginning of each day, the probability of flooding was determined from Eq. 2 and used for the four time steps comprising that day. For each time step, a generated random number was compared to the day's probability of flooding. If the random number was less than the probability of flooding, the simulated marsh was assumed flooded. Tidal stages were updated to reflect the higher water levels associated with flooding (falling and low were updated to rising; rising and high were updated to
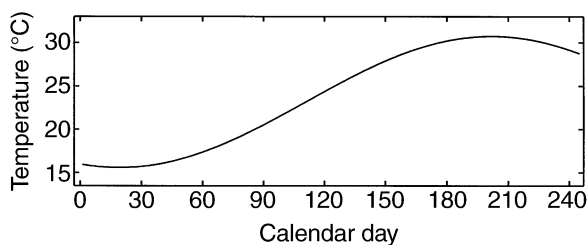

FIG. 3. Daily water temperature used in model simulations. The function used to calculate the simulated daily water temperature was estimated from water temperatures measured in shallow Louisiana (USA) marshes, 1970–1997.
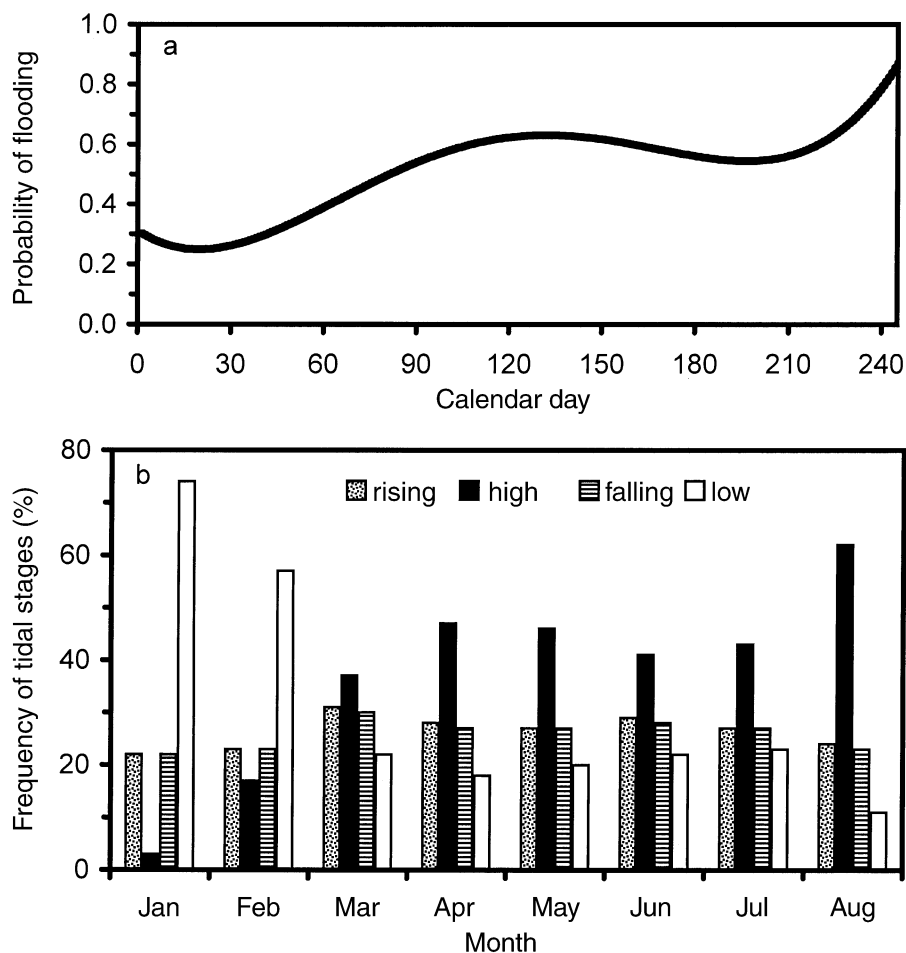
FIG. 4.   Marsh inundation. (a) Probability of marsh flooding used in model simulations. (b) The resulting frequency of the four tidal stages, summarized by month, for a baseline simulation.

high). If the marsh was determined to be not flooded for the time step, then the tidal stages were updated to reflect the lowered water levels (falling and low were updated to low; rising and high were updated to falling). All cells on the spatial grid exhibited the same tidal stage on any given time step. A representative series of resulting tidal stages for one simulation, summarized as the frequency of occurrence by month, is shown in Fig. 4b.

Introduction of postlarval shrimp

Individual shrimp were tracked from the time they entered the marsh as postlarvae until they either died or reached 70-mm total length, which is a typical size when brown shrimp emigrate from estuarine marshes into offshore waters (Knudsen et al. 1985). It was unnecessary to include shrimp from other year classes because the brown shrimp population consists almost entirely of organisms less than one year old (Caillouet et al. 1980). When postlarvae arrive in the estuarine nursery areas, they are generally 10–15 mm in total length (Baxter and Renfro 1967, Minello et al. 1989).

Each simulated shrimp was randomly assigned an initial length from a normal distribution (mean = 15.0 mm, standard deviation = 2.5, minimum = 5.0, maximum = 25.0). Shrimp were initially randomly distributed among water cells that were 2 m or less from the edge (i.e., Water1 or Water2 cells).

Simulated shrimp entered the model in weekly cohorts. Cohort strength was derived from 28 years (1970–1997) of weekly postlarval density data (number of postlarval shrimp/m^3) collected by the LDWF (Fig. 5). Relative weekly cohort strength was computed from the field data as the weekly mean density divided by the total sum of weekly mean densities. The number of shrimp introduced in each simulated weekly cohort was calculated by multiplying the specified total number of postlarval shrimp in each simulation by the relative weekly cohort strength. The total number of postlarval shrimp in the baseline simulations was set at 100 000 postlarvae so that the maximum mean simulated density (20.8 shrimp/m^2 at high tide in Veg1 cells during spring) was similar to maximum reported field
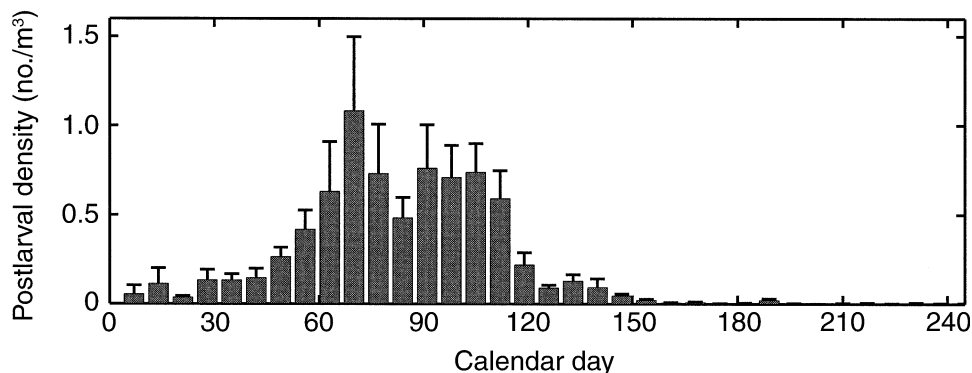
Fig. 5. Weekly postlarval shrimp densities (mean and 1 SE) from data collected in Barataria Bay, Louisiana, USA, by the Louisiana Department of Wildlife and Fisheries from 1970 to 1997.

estimates (21.1 shrimp/m², Zimmerman and Minello 1984; 24.7 shrimp/m², Rozas and Zimmerman 2000).

Movement

We used field observations to derive a set of movement rules to mimic shrimp movement patterns over tidal cycles and on meter spatial scales (right side of Fig. 1). Because shrimp rarely penetrate farther than 3 m into the vegetation (Peterson and Turner 1994, Minello and Rozas 2002), we limited all shrimp movement to vegetated cells that were within 3 m of the water (i.e., Veg1, Veg2, and Veg3 cells). In order to provide enough habitat for shrimp located near the sides of the habitat maps, shrimp were allowed to wrap around the sides of the maps.

Shrimp movement was simulated by determining how far a shrimp could move from its present location (i.e., a neighborhood of cells), identifying viable candidate cells from the neighborhood, and then selecting an individual cell from the viable candidate cells. As shrimp grew longer, their motility increased ($m = 1$ for <30-mm-long shrimp, $m = 2$ for 30–45 mm shrimp, and $m = 3$ for >45-mm shrimp). Motility (m) was used to define the neighborhood of cells. During each 6-h time step, the neighborhood of cells was defined for each shrimp as number of cells (n) in all eight directions (i.e., including the diagonal directions). The neighborhood was defined as $n = m$, unless shrimp were moving between water cells or to the vegetated edge; then their faster swimming (Minello et al. 1990) was simulated by expanding the neighborhood to $n = 3m$. Identifying the viable candidate cells from among the neighborhood of cells depended on the tidal stage. During a low tide, shrimp could only move to water cells within the neighborhood. During a rising or high tide, shrimp could move to any cell in the neighborhood that was within 3 m of the edge. During a falling tide, shrimp could move to water cells or to vegetated cells within m meters of the edge. Simulated shrimp moved to the candidate cell that provided the best expected growth rate (based on cell habitat type and local shrimp den-

sity). Juvenile brown shrimp are found at higher densities in vegetated edges than in open water or in interior vegetation (Minello 1999, Rozas and Zimmerman 2000). Ties in the best expected growth rate were settled by random selection among the tied cells. If none of the expected growth rates in the neighboring cells was higher than the current cell, the shrimp did not move.

Mortality

Predation mortality was influenced by shrimp length, movement, and the habitat type of its cell. Realized instantaneous mortality rate (RZMORT, per 6-h tidal stage) was calculated by multiplying a baseline mortality rate by a size-based modifier (M_s), a habitat-based modifier (M_h), and a movement-based modifier (M_m):

$$\text{RZMORT} = \text{BZMORT} \times M_s \times M_h \times M_m. \quad (3)$$

Field estimates for realized instantaneous mortality rates for 6-h time periods for all size classes of juvenile brown shrimp in the northern Gulf of Mexico average near 0.007 (see Minello et al. 1989). We used a baseline instantaneous mortality rate (BZMORT) of 0.005 per 6-h time step, assumed to apply to a 30-mm-long shrimp in vegetated habitat. We used a lower baseline rate than estimated from field studies because field estimates were the average over all habitat types, whereas we assumed the baseline rate represented the low-mortality vegetated habitat. Mortality rate of brown shrimp declines as shrimp size increases (Minello et al. 1989); hence, the size-based modifier (M_s) decreased with increasing shrimp length, L (Fig. 6a):

$$M_s = 53.092 \times L^{-1.1163}. \quad (4)$$

Because predation rates are higher in nonvegetated areas than in areas with vegetative structure (Minello et al. 1989, Minello and Zimmerman 1983), the habitat-based modifier (M_h) was increased from 1.0 for shrimp in vegetated cells to a value of 2.0 when shrimp were in water cells. Because moving shrimp may be more vulnerable to predation (see Minello et al. 1987), the
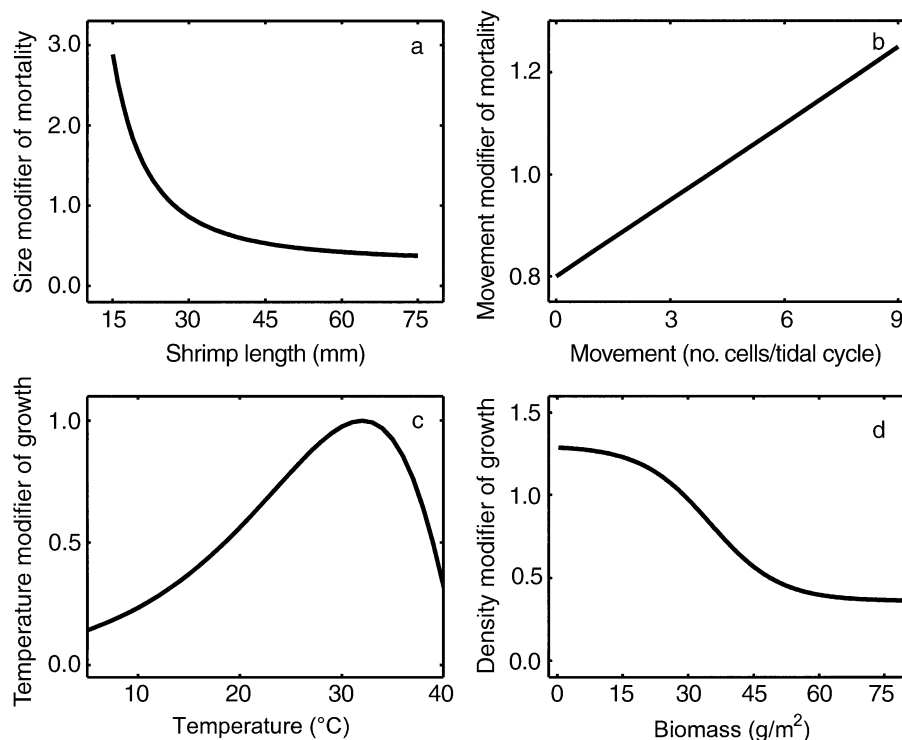
FIG. 6. Functions that modified mortality and growth used in model simulations. (a) Size modifier of mortality rate, M_s. (b) Movement modifier of mortality rate, M_m. (c) Temperature modifier of growth rate, M_t. (d) Shrimp density modifier of growth rate, M_d.

movement-based modifier (M_m) increased with the number of cells moved in each tidal stage (Fig. 6b):

$$M_m = (\text{NMOVED} \times 0.05) + 0.95 \qquad (5)$$

where NMOVED is the number of cells moved by the shrimp during the current tidal stage. The probability of dying (PROBD) during a single tidal stage (6 h) was calculated from the realized instantaneous mortality rate as PROBD $= 1.0 - e^{-\text{RZMORT}}$. We generated a uniform random number between 0 and 1, and if it was less than PROBD, then the shrimp was considered dead.

Growth

Simulated shrimp growth depended on water temperature, habitat type of the shrimp's cell, and the local shrimp density. Estimates for juvenile brown shrimp growth rates in the northern Gulf of Mexico vary from 0.1 to 3.3 mm/d (see Louisiana Department of Wildlife and Fisheries 1992). The average baseline growth rate (BGROW) in model simulations was set to 0.25 mm per six hours (1 mm/d). Each simulated shrimp was randomly assigned a baseline growth rate from a normal distribution (mean = BGROW, standard deviation = $0.25 \times$ BGROW, minimum = 0.25, maximum 2.25). Shrimp maintained their BGROW throughout the simulation. Realized growth rates of each shrimp (RGROW) varied throughout the simulation and were

computed as the baseline rate times a temperature-based modifier (G_t), a habitat-based modifier (G_h), and a density-based modifier (G_d):

$$\text{RGROW} = \text{BGROW} \times G_t \times G_h \times G_d. \qquad (6)$$

The temperature-dependent growth modifier (G_t) was derived to allow fastest growth at optimal temperatures. For shrimp between 10 and 50 mm, growth rates are slow (e.g., 0.08–0.46 mm/d) at 18°C and faster (e.g., 0.85–1.35 mm/d) at 32°C (Zein-Eldin and Aldrich 1965). The temperature modifier for growth was created from an equation used to describe temperature-dependent consumption for fish in warm water (Hewett and Johnson 1987). The modifier increases with increasing temperature until maximum growth is achieved at optimal temperature (32°C), and the modifier declines to zero at a maximum temperature (40°C). A third parameter ($\theta = 2.5$) controls the shape of the curve, which is shown in Fig. 6c.

The habitat-dependent growth modifier (G_h) was derived to allow faster growth in the resource-rich vegetated cells. Brown shrimp have faster growth rates when in cages with vegetation compared to cages without vegetation (e.g., 0.98 mm/d vs. 0.77 mm/d, respectively, at high shrimp densities; 1.41 mm/d vs. 1.03 mm/d, respectively, at low densities) (Minello and Zimmerman 1991). Based on these estimates, the habitat modifier was assigned a value of $G_h = 1.0$ for shrimp

in water cells and a value of $G_h = 2.0$ for shrimp in vegetated cells.

The density-dependent growth modifier (G_d) was derived to allow faster growth in cells with fewer shrimp. Brown shrimp grow faster when in very low densities (1.41 and 1.03 mm/d at densities of 2.0 and 2.2 shrimp/m², respectively) and slower when in higher densities (0.98 and 0.77 mm/d at densities of 7.8 and 8.9 shrimp/m², respectively) (Minello and Zimmerman 1991, T. J. Minello, *unpublished data*). Related species of farmed penaeid shrimp (*Penaeus setiferus* and *P. vannamei*) have an inverse relationship between growth and stocking density (Williams et al. 1996). We made the relationship between shrimp density and growth rate linear over most densities and asymptotic at extreme low and extreme high densities (Fig. 6d):

$$G_d = 1.3 - \frac{0.94}{1 + \exp\left[-\left(\dfrac{\text{BIOMASS} - 35.0}{7.9}\right)\right]} \quad (7)$$

where BIOMASS is the density of shrimp in the cell in total grams. Biomass density was computed as the sum of individual shrimp masses in each cell, with mass (in grams) determined from length (*L*, in millimeter) using $MASS = 0.0000037 \times L^{3.16}$ (based on Parrack 1979). We used biomass, rather than numbers of individuals, because biomass better reflects the total consumptive demand of all of the shrimp in a cell.

ANALYSIS

Relationships between individual characteristics and survivorship

We contrasted the characteristics of shrimp that survived to 70 mm with those of shrimp that died, in a single simulation of baseline conditions on the high-edge, high-vegetation (HE–HV) habitat map. We compared the mean realized daily growth rate, mean number of cells moved per tidal stage, mean percentage of time spent in vegetated cells, and mean number of cellmates between survivors and those that died. Because shrimp growth, mortality, and movement depended on habitat type, we expected differences in the characteristics between survivors and nonsurvivors. The utility of this analysis is that it allowed us to estimate the magnitude of differences in these characteristics.

Relationships among vegetation, vegetated edge, and survival

We simulated shrimp survival on each of the four habitat maps. The analysis can be viewed as a 2×2 factorial design, with the amount of edge as one factor and the amount of vegetation as the second factor. The four maps also represent snapshots in a simplified continuum of marsh disintegration (i.e., LE–HV to HE–HV to HE–LV to LE–LV). By evaluating the patterns of predicted survival among these four habitat maps, hypotheses can be formed and evaluated regarding the effect of marsh disintegration and restoration on juvenile brown shrimp survival.

Model behavior

Comparison with field data.—Rigorous validation of the simulation model using independent field data was not possible because of the difficulties in observing annual shrimp survival in different marshscapes under identical biological conditions (e.g., larval supply) and environmental conditions (e.g., water temperature and flooding regimes). In order to increase confidence in our results, we corroborated the model by comparing model predictions to temperature-classified annual shrimp abundance estimates, fine-scale shrimp density patterns, and stable isotope values.

1. *Abundance and temperature.*—The first comparison examined predicted and field-observed differences in brown shrimp abundances between cold and warm years. Temperature and survival were linked in the model through the temperature-dependent growth multiplier G_t and the size-dependent mortality multiplier, M_s. Warmer temperatures allowed faster growth, and faster growth allowed shrimp to spend less time in smaller size classes that had higher mortality rates. The observed estimates were calculated from weekly monitoring data collected over 28 years (1970–1997) by the Louisiana Department of Wildlife and Fisheries (LDWF; Baton Rouge, Louisiana, USA). Haas et al. (2001) summarized portions of these monitoring data in order to obtain average annual indices of shrimp abundance and water temperature. We divided their annual indices of mean water temperature in coastal bays roughly in half into cold and warm years. The mean number of shrimp caught per tow of a 16-foot (4.88 m) otter trawl was calculated for the years assigned to warm and cold temperature groups. Comparable predictions from the model (i.e., percentage of shrimp surviving to 70 mm) were generated by running the model on the high-edge, high-vegetation habitat map under cold (1.0°C subtracted from baseline) and warm (1.0°C added to baseline) conditions. We compared the variation in observed annual shrimp abundances with the variation in predicted annual survival across the two temperature groups.

2. *Density patterns.*—The second corroboration comparison examined predicted and field-observed, fine-scale, brown shrimp density patterns. We used the results from the baseline simulation on the high-edge, high-vegetation map and plotted the density of shrimp at each tidal stage (low, rising, falling, high) in each habitat type (Water1, Water2, Water3, Water>3, Veg1, Veg2, Veg3, Veg>3 [see Table 1 for definitions]) against the calendar day. We then compared predicted and field-reported density patterns. Examining density patterns is an excellent way to corroborate the model because simulated density patterns were not directly specified in the model.
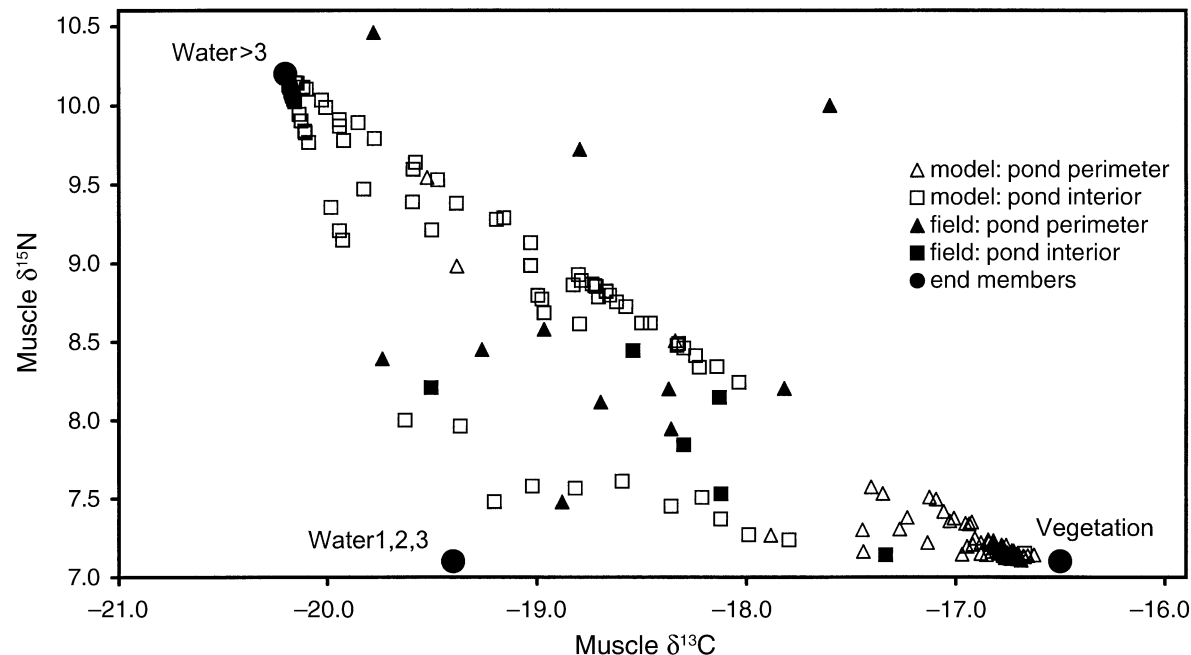
FIG. 7. Predicted (model) and observed (field) $\delta^{13}C$ and $\delta^{15}N$ in muscle tissue from individual shrimp sampled from pond perimeter and pond interior locations. Solid black circles are used to define the three end members (vegetation, pond perimeter, and pond interior) used to calculate the isotope values of simulated shrimp. Predicted values are 200 randomly selected shrimp, all >30 mm in length, during May in the model simulation, with about half of the shrimp taken from pond perimeter and half from pond interior habitats.

3. *Stable isotopes.*—The third corroboration compared predicted and measured stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values in the muscle tissue of individual brown shrimp. Shrimp acquire their stable isotopic $\delta^{13}C$ and $\delta^{15}N$ compositions from their diets. Because diets are often habitat specific, movement between habitats may be detected as changes in stable-isotope values. Metabolism and growth alter isotopic compositions so isotope values in shrimp muscle tissue reflect a combination of very recent diet and a longer-term past diet. Fry et al. (2003) measured $\delta^{13}C$ and $\delta^{15}N$ in the muscle of individual shrimp in four ponds in a Louisiana marsh. The measurements were for shrimp collected in April and May 2000, and the habitat of capture (pond interior or perimeter) was recorded for each shrimp analyzed. We incorporated $\delta^{13}C$ and $\delta^{15}N$ dynamics in the model, and simulated shrimp isotopes for one of the ponds sampled by Fry et al. (2003). We then predicted shrimp $\delta^{13}C$ and $\delta^{15}N$ values and compared these values to the measured values.

Stable-isotope values for individual shrimp were modeled by calculating the accumulated isotope value for $\delta^{13}C$ and for $\delta^{15}N$ for each individual shrimp. The calculation was basically a weighted mean of the new dietary value and the previous isotopic value for shrimp muscle (discounted by a metabolic constant):

$$S_{t+1} = \{(W_t \times S_t) - (\tau \times W_t \times S_t)$$

$$+ [(W_{t+1} - W_t) + \tau \times W_t] \times D_{t+1}\}/W_{t+1} \quad (8)$$

where S_t is the isotope value ($\delta^{13}C$ or $\delta^{15}N$) of the shrimp

muscle at time t; W_t is the mass in grams of the shrimp at time t; D is the isotope value of a dietary end member (determined by habitat type of the cell); and τ is the metabolic turnover constant (per six hours). Initial values of $\delta^{13}C$ and $\delta^{15}N$ were set to values characteristic of water-column feeding by postlarvae ($\delta^{13}C$ = -20.2‰ and $\delta^{15}N$ = 10.2‰, Fry et al. 2003). We estimated a value for the metabolic turnover constant (τ) based on the results of brown shrimp diet-switching experiments reported in Fry and Arnold (1982). We applied Eq. 8 to the conditions in their experiment and, using repeated trial-and-error simulation, determined a value for τ (-0.0008) that resulted in predicted declines in $\delta^{13}C$ matching the measured declines in the experiment. We used a slightly slower value (0.75τ) for the metabolic turnover constant for $\delta^{15}N$ because N may be more conserved in animal metabolism than C. We specified $\delta^{13}C$ and $\delta^{15}N$ values for three dietary end members (Fig. 7) to represent three common habitat types: vegetation (Veg1, Veg2, Veg3, and Veg>3 cells), pond perimeter (Water1, Water2, and Water3 cells), and pond interior (Water>3 cells). We used the simulation model, with Eq. 8 added, to simulate shrimp under baseline conditions on a habitat map which was derived from an image of Fry et al.'s (2003) Pond 1A. Similarity between predicted and observed stable isotopes would imply that the model was simulating fine-scale resource acquisition that was consistent with the stable isotopes.

TABLE 2.   Characteristics of shrimp that survived to 70 mm length (30.22% of total) and those
that died during the simulation (69.78% of total).

Shrimp status	Realized growth rate (mm/d)	No. cells moved per tidal stage	Time spent in vegetation (%)	Local density (no. shrimp/cell)
Survivors	1.35	3.16	73.21	11.29
Non-survivors	0.71	7.21	46.88	10.15

Note: Mean values of the characteristics are based on the results of a single baseline simulation
using the high-edge, high-vegetation (HE–HV) habitat map.

Robustness of model predictions.—We investigated
the robustness of model predictions by repeating the
simulations on the four habitat maps with higher initial
numbers of postlarvae (300 000 and 600 000 vs.
100 000 used in baseline conditions), and with three
alterations of the movement rules. In the first altered-
movement simulation, the movement rules were mod-
ified by omitting the size dependency of movement.
Motility (m) was set to 2 for all sizes of shrimp, which
increased the distance evaluated by shrimp <30 mm
long ($m = 1$ in baseline) and decreased the distance
evaluated by shrimp >45 mm long ($m = 3$ in baseline).
In the second altered-movement simulation, we dou-
bled the size of the neighborhood of candidate cells
available for movement (i.e., we doubled the value of
n). In the third altered-movement simulation, the move-
ment rules were modified by selecting a destination cell
randomly rather than based on the best expected growth
rate. We compared the predicted survival across the
four habitat maps for the each of the increased numbers
of postlarvae simulations and the three altered-move-
ment simulations.

RESULTS

Relationship between individual characteristics and survivorship

Shrimp that survived to length of 70 mm grew faster,
moved less, spent more time in vegetation, and expe-
rienced slightly higher local shrimp densities than
shrimp that died during the simulation (Table 2).
Growth rates and time spent in vegetation were nearly
twice as high for survivors as for non-survivors, and
the magnitude of movement (number of cells moved)
was about half as much for survivors as for non-sur-
vivors. Surviving shrimp were found in slightly denser
assemblages than non-survivors. Even though high
densities decrease growth rates, survivors apparently
benefited from clustering in areas of optimal habitat
(i.e., the increase in growth due to access to vegetation
outweighed the decrease in growth due to high shrimp
densities).

Relationships among vegetation, vegetated edge, and survival

Shrimp survival was higher in maps with more edge
habitat (roughly 30% survival in high-edge habitats vs.
23% survival in low-edge habitats, Table 3). Habitat
maps with more vegetation supported negligibly more

survival (1–2% more) than did habitats with less veg-
etation. Compared to the two low-edge habitat maps,
the two high-edge habitat maps produced survivors to
70 mm that grew only slightly faster (1.37 and 1.34
mm/d in high-edge vs. 1.33 mm/d in low-edge), moved
substantially less (3.14 and 3.27 cells vs. 5.08 and 5.60
cells per tidal stage, respectively), spent moderately
more time in the vegetation (76 and 71% vs. 69 and
66%, respectively), and experienced lower local den-
sities (11.40 and 12.77 shrimp/cell vs. 17.31 and 19.87
shrimp/cell, respectively). If the habitat maps are
viewed as a continuum of marsh disintegration, shrimp
survival peaked at the intermediate levels of marsh
disintegration when edge habitat was highest.

Model behavior

Comparison with field data.—

1. *Abundance and temperature*.—Both the model
and field data showed a pattern of higher shrimp abun-
dance under warmer annual temperatures. The number
of shrimp caught per tow increased from ~61.3 shrimp
in cold-temperature years to 96.2 shrimp in warm-tem-
perature years. Shrimp survival was predicted to be
lower (27.9%) in the simulation with lowered temper-
atures and higher (35.0%) in the simulation with the
elevated temperatures. Observed average shrimp abun-
dance was 1.5 times higher in warm vs. cold years,
which was similar to predicted survival being 1.25
times higher in warm vs. cold years.

2. *Density patterns*.—Simulated patterns of shrimp
density (Figs. 8 and 9) were similar to field-observed
patterns. Simulated shrimp were absent and observed
shrimp were rare in vegetated cells at low tide (Kneib
1997). Shrimp densities were highest during April in
model simulations (mean monthly densities at high tide
for Veg1 cells was 12.8 shrimp/m^2 in March, 15.9
shrimp/m^2 in April, and 4.1 shrimp/m^2 in May), and
highest during late March and early April in field ob-
servations (Baxter and Renfro 1967, Trent et al. 1976,
Zimmerman et al. 1984). The annual mean simulated
shrimp density (during rising, high, and falling tidal
stages) for shrimp in all vegetated cells was 8 times
the mean density in water cells. Estimated ratios of
shrimp densities in vegetated to non-vegetated areas
average about 4:1 (Minello 1999), and can be as high
as 22:1 (Zimmerman et al. 1984). Finally, annual mean
simulated shrimp density during high tide in Veg1 cells
(edge) was 2.79 times the average density in Veg3 cells

TABLE 3. Model predictions of survival, growth rate, movement, time in vegetation, and local density of shrimp surviving to a length of 70 mm on four habitat maps that represent a progression of marsh disintegration.

Habitat maps, by initial no. of postlarvae†	Survival to 70 mm (% of total shrimp)	Growth rate (mm/d)	No. cells moved per tidal stage	Time spent in vegetation (%)	Local density (no. shrimp/ cell)
1×10^5 postlarvae					
LE–HV	23.52 (4.3)	1.33 (0.8)	5.08 (9.1)	69.04 (3.3)	19.87 (4.1)
HE–HV	31.04 (4.6)	1.37 (2.1)	3.14 (5.1)	76.06 (5.0)	11.40 (3.5)
HE–LV	28.82 (4.9)	1.34 (1.1)	3.27 (6.0)	71.00 (4.5)	12.77 (6.2)
LE–LV	22.81 (4.8)	1.33 (1.5)	5.60 (8.0)	66.54 (5.1)	17.31 (7.3)
3×10^5 postlarvae					
LE–HV	18.87	1.14	6.65	68.12	51.90
HE–HV	29.25	1.30	3.56	76.45	33.87
HE–LV	27.68	1.22	3.56	74.62	36.68
LE–LV	18.53	1.18	6.38	67.46	43.02
6×10^5 postlarvae					
LE–HV	15.81	0.97	4.84	50.94	59.40
HE–HV	23.09	1.08	3.91	72.62	59.86
HE–LV	21.66	1.00	3.21	65.84	50.67
LE–LV	15.03	1.00	5.15	48.42	55.03

† Maps represent habitats with low edge (LE), high edge (HE), low vegetation : water ratios (LV), and high vegetation : water ratios (HV). The mean and CV (shown in parenthesis) were produced by repeating each simulation five times with identical input parameters but with different random-number sequences. The statistics (mean with CV shown in parentheses) from the simulations with baseline initial number of postlarvae (1×10^5) were produced by repeating each simulation five times with identical input parameters but with different random-number sequences. The statistics from the simulations with the two higher-than-baseline initial number of postlarvae (3×10^5 and 6×10^5) are from a single model simulation.
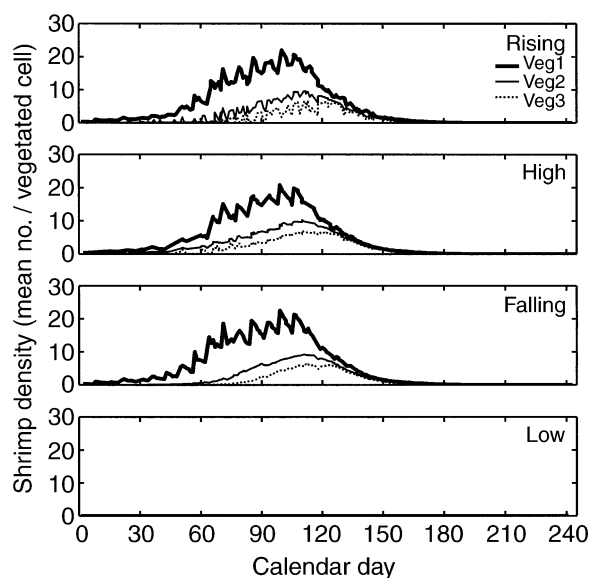
FIG. 8. Simulated average brown shrimp density in vegetated cells at each of four tidal stages for every day of a baseline simulation of the high-edge and high-amount-of-vegetation (HE–HV) map. In general, the heavier lines are closer to the vegetation–water edge. Thick, solid lines represent shrimp densities in vegetated cells near the edge (Veg1 cells); thin, solid lines represent shrimp densities in vegetated cells ~2 m from edge (Veg2 cells); and dotted lines represent shrimp densities in vegetated cells ~3 m from the edge (Veg3 cells).
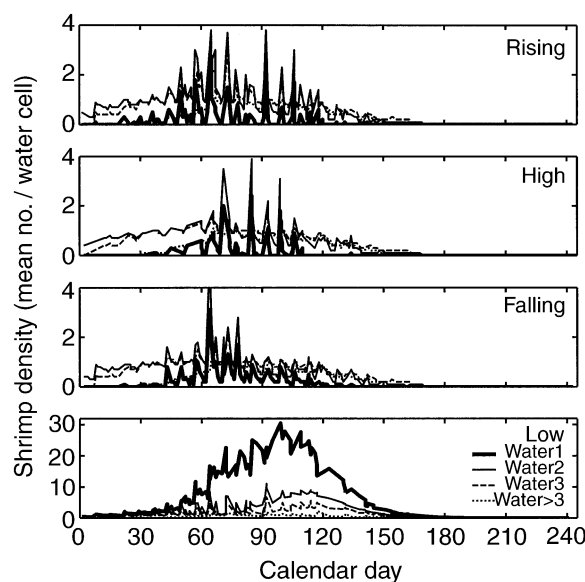
FIG. 9. Simulated average brown shrimp density in water cells at each tidal stage for every day of a baseline simulation of the high-edge and high-amount-of-vegetation (HE–HV) map. In general, the heavier lines are closer to the vegetation–water edge. Thick, solid lines represent shrimp densities in water cells near the edge (Water1 cells); thin, solid lines represent shrimp densities in water cells ~2 m from the edge (Water2 cells); dashed lines represent shrimp densities in water cells ~3 m from the edge (Water3 cells); and dotted lines represent shrimp densities in water cells >3 m from the edge (Water>3 cells). Note the higher densities on the y-axis in the bottom (low tide) panel.

(interior). Minello and Rozas (2002) estimated an edge: interior ratio of shrimp densities of 2.77.

3. *Stable isotopes.*—Simulated shrimp sampled in May in the pond-perimeter habitat had $\delta^{13}C$ and $\delta^{15}N$ values that suggested their food resources relied more on vegetation than was suggested by the field-measured isotopes (Fig. 7). Many simulated $\delta^{13}C$ and $\delta^{15}N$ values were associated with the vegetation end member, whereas the values for the field-collected shrimp fell more towards the center of the end-member triangle, indicating a more diverse diet. It is difficult to evaluate the predicted $\delta^{13}C$ and $\delta^{15}N$ for the shrimp sampled in the interior-pond habitat because of limited observations.

Robustness of model predictions.—Three- and six-fold increases in initial postlarval density did not change the patterns of survival across the four habitat maps, and in most cases it did not change the patterns of survival characteristics of individuals documented under baseline densities (Table 3). Regardless of the initial number of postlarvae, high-edge habitat maps produced higher shrimp survival and shrimp that moved less and spent more time in vegetation. The baseline pattern of high-edge maps producing higher realized growth rates and less dense assemblages of shrimp became slightly diluted under the highest (600 000) initial postlarvae conditions. Increasing post-larval numbers resulted in density-dependent growth causing slower growth rates, higher mortality, and slightly decreased time spent in vegetation. There was no clear relationship between increasing initial number of postlarvae and the amount of shrimp movement.

Although altering the movement rules affected the magnitude of predicted survival, the pattern of greater survival with increased edge habitat was insensitive to our changes in movement rules (Table 4). Altering the movement rules so that movement was independent of size (i.e., constant motility) affected the pattern of high-edge maps producing survivors that spent more time in vegetation. Doubling the neighborhood of cells available for movement (i.e., doubling n) increased movement and negligibly decreased survival. Selecting a destination cell randomly, rather than based on the best expected growth rate, substantially decreased the survival in all four habitat maps. Random movement reduced growth rates and disrupted the pattern of decreased densities in the high-edge habitats. Nevertheless, for the three changes in movement rules we examined, shrimp had higher survival, moved less, and had slightly higher growth rates on high-edge maps than on low-edge maps.

DISCUSSION

Brown shrimp movement and habitat preference

The movement rules represent the most speculative aspect of the model. The general pattern of migration over a brown shrimp's entire life cycle is well docu-

mented (see Cook and Lindner 1970), and tagging studies have provided information on movement over weeks to months (e.g., Clark et al. 1974, Sheridan et al. 1989). Much less is known about how individual shrimp move on fine spatial (meters) and temporal (daily or finer) scales because of difficulties tracking small, aquatic organisms.

Simulated shrimp showed a strong preference for vegetated habitats, which agrees with the field data on fine-scale shrimp density patterns but differs from the implications of the stable-isotope data. In the second corroboration comparison, both simulated and observed shrimp densities were higher in vegetation than in open water. The strong preference for vegetated habitats in the simulations, however, differs from the habitat-preference patterns implied by the stable-isotope values in the third corroboration comparison. Predicted $\delta^{13}C$ and $\delta^{15}N$ in shrimps inhabiting pond-perimeter habitat during May showed greater reliance on vegetation than indicated by the observed isotope values (Fig. 7).

We could have reconciled the observed and simulated isotope results by changing the movement rules so that shrimp spent less time in vegetated habitat, but we decided not to change the rules for several reasons. First, the sample size for the stable-isotope determination was small (17 shrimp) and was centered on one small (100 × 100 m) geographic area, whereas the field data on fine-scale density patterns represented average densities across much larger areas. Second, the strong association of simulated shrimp with vegetation is seasonal, and stable isotopes in simulated shrimp during months other than May showed values more similar to observed isotope values. Third, the determination of the $\delta^{13}C$ and $\delta^{15}N$ for the three dietary end members (determined by their habitat type: vegetation, pond perimeter, pond interior) was somewhat arbitrary. Overall, the discrepancy between the predicted and observed isotope values highlights the uncertainty regarding interpreting stable-isotope values and simulating fine-scale movement. Additional coordinated studies between movement modeling and stable isotope-measurements in the field are needed.

Edge habitat and predicted survival

Marshes with more edge habitat supported higher shrimp survival than marshes with less edge habitat. This result was robust when the initial numbers of post-larval shrimp were 3 and 6 times baseline, when movement was not related to size, when potential movement distance was doubled, and when movement was random rather than directed toward cells with higher growth rates (Tables 3 and 4).

The pattern of increased shrimp survival with increased edge habitat is consistent with correlative studies. Browder et al. (1989) described a positive correlation between annual shrimp catch and an annual estimate of the amount of edge habitat. Faller (1979)

TABLE 4. Model predictions of survival, growth rate, movement, time in vegetation, and local density of shrimp on four habitat maps under baseline conditions and for three alterations of the movement rules.

Habitat maps by change in movement	Survival to 70 mm (% of total shrimp)	Realized growth rated (mm/d)	No. cells moved per tidal stage	Time in vegetation (%)	Local density (no. shrimp/ cell)
Baseline					
LE–HV	23.52	1.33	5.08	69.04	19.87
HE–HV	31.04	1.37	3.14	76.06	11.40
HE–LV	28.82	1.34	3.27	71.00	12.77
LE–LV	22.81	1.33	5.60	66.54	17.31
Constant motility					
LE–HV	24.75	1.36	5.39	75.07	25.66
HE–HV	29.67	1.37	4.14	76.31	12.77
HE–LV	27.44	1.36	3.88	72.16	13.40
LE–LV	22.21	1.34	6.95	69.92	19.73
Doubled neighborhood					
LE–HV	21.69	1.37	9.19	74.14	21.62
HE–HV	27.64	1.42	5.09	76.25	9.58
HE–LV	28.37	1.39	5.78	76.62	11.51
LE–LV	21.72	1.37	8.18	70.43	17.32
Random destination					
LE–HV	9.43	1.08	8.09	19.06	6.43
HE–HV	15.19	1.13	4.15	31.00	6.04
HE–LV	12.37	1.09	5.70	22.53	4.39
LE–LV	9.53	1.06	7.36	17.52	5.40

Note: The baseline results are the mean of five replicate simulations; the results of the altered movement simulations are from single model simulations. Maps represent habitats with low edge (LE), high edge (HE), low vegetation : water ratios (LV), and high vegetation : water ratios (HV). Movement rules were altered such that: (1) shrimp motility remained constant regardless of shrimp size (constant motility), (2) the size of the neighborhood of cells available for movement was doubled (doubled neighborhood), and (3) destination cell was randomly selected rather than based on growth rate (random destination).

described a correlation between shrimp harvest and the area of marsh that has a threshold amount of edge habitat. Minello and Rozas (2002) used fine-scale density patterns and landscape-scale analyses of Galveston Bay (Texas, USA) wetlands to show the positive relationship between the amount of marsh edge habitat and shrimp abundance and to simulate an increase in shrimp densities by adding creeks to solid marsh vegetation.

The characteristics of surviving shrimp in model simulations offer evidence of what may cause the patterns of brown shrimp survival documented in descriptive and correlative studies. Field studies show that shrimp are generally concentrated in edge habitat, and several reviews hypothesize that shrimp in vegetation benefit from increased growth due to abundant food supplies and from decreased mortality due to structural protection from predators (Zimmerman et al. 2000). In our simulations, the survivors in high-edge habitats, as compared to low-edge habitats, moved less, spent more time in vegetation, were in less-dense configurations, and had negligibly higher growth rates (Table 3). High-edge habitats increased survival by providing shrimp more direct access to vegetation. In low-edge habitats, simulated shrimp had less access to the high growth rates and low mortality rates of vegetated areas and therefore also encountered additional movement-related mortality and density-dependent growth costs.

We performed several additional simulations to further explore mechanisms that led to increased survival in high-edge habitat maps. In one set of simulations we held the habitat-dependent growth modifier constant between vegetated and non-vegetated areas; in another we held the habitat-dependent mortality modifier constant; and in a third we held both the habitat-dependent growth and mortality modifiers constant. In all three cases, the highest survival occurred in the high-edge habitat maps, even though the highest realized growth rates sometimes occurred in the low-edge habitat maps. The only attribute that remained constant across all simulations was that shrimp in high-edge habitat maps always spent more time in vegetation. Field and manipulative studies that examine how shrimp growth and movement are affected by habitat and local shrimp densities are warranted.

While growth rate is a relatively easy-to-measure and popular indicator of habitat quality (Meng et al. 2001), our results suggest that for brown shrimp, field-measured growth rates alone may not be a sensitive indicator of habitat quality. Several observations led to this conclusion. First, the simulated survivors in high-edge habitats had only negligibly higher realized growth rates than did survivors in low-edge habitats (Table 3). Second, when growth rates were held constant between habitat types, there were still consistent differences in

survival between high-edge and low-edge habitat maps. Finally, density-dependent and spatially explicit processes can cause significant differences between potential growth rates and realized growth rates. This difference can be important because field studies typically measure an index of potential growth rate, which may not accurately reflect realized growth rates; yet, it is realized growth rates that influence population dynamics.

Management implications

The difference in survival among the habitat maps was small but potentially important to shrimp population dynamics. Predicted survival to 70-mm length was consistently higher in high-edge habitats, with differences in survival between high-edge and low-edge habitats on the order of 5–10%. These small differences in survival may be biologically important given that the total range of survival in model simulations is only about five-fold. Under the optimal environmental conditions of high growth rates and low mortality rates of vegetated habitat applied to all shrimp at all times, simulated shrimp on the low-edge, low-vegetation habitat map increased from 22% to ~50%. At the other extreme, when growth and mortality rates were set to values typical of open-water conditions at all times, simulated shrimp survival on the same habitat map decreased to ~10%. Thus, even under these unrealistically extreme good and bad conditions, the maximum range in predicted survival only varied from 10 to 50%, which implies that the simulated difference of 10% in survival among the four habitat maps is likely to be biologically important. Additionally, the range in the amount of edge in the four habitat maps we used is narrower than the range observed in nature, so larger differences in survival than we predicted are expected if the model was applied to the full range of marsh configurations.

A 5–10% difference in survival for the juvenile stage may seem small but can have important fishery implications. Small changes in the percentage of estuarine survival can translate into significant changes in recruitment to the fishery. The spatial extent of our simulations was small ($10\,000$ m^2), but if allowed to represent average marsh conditions, very rough predictions can be made about changes in survival over larger spatial scales. For example, under baseline conditions on the $10\,000$-m^2 habitat maps, approximately $5\,000$ more shrimp (total mass: 20.4 kg [45 pounds]) survived in high-edge habitats than in low-edge habitats. If this increase in survival is scaled up to represent the entire state (available habitat $\cong 800\,000$ ha, Barrett and Gillespie 1973), the difference in survival between high-edge habitats and low-edge habitats becomes a difference of about 4×10^9 shrimp weighing 16.3×10^6 kg (36 million pounds), which is of the same magnitude as the annual Louisiana landings of 15.4×10^6 to 32.2×10^6 kg (34–71 million pounds) during 1970–2001

(data available online at NOAA Commercial Fishery Landing Database website).[8]

Because brown shrimp survival is related to edge habitat and marshes are being lost throughout the Gulf coast, the management of brown shrimp should be extended from the current practice of protecting the spawning stock through catch regulations to also protecting the estuarine life stages through habitat conservation and restoration. The dome-shaped relationship between edge habitat and marsh disintegration (Browder et al. 1985) suggests that the area of productive high-edge habitats will peak during intermediate levels of marsh disintegration. If marsh disintegration continues past intermediate levels, estuarine marshscapes may shift from predominantly high-edge habitats to low-edge habitats (Browder et al. 1989). The results of our present study suggest such a shift would be accompanied by a decrease in the estuarine production of shrimp. The growing interest in defining essential fish habitat should be accompanied by continued spatially explicit modeling of critical biological processes.

Given the potential importance of edge habitat to the survival of brown shrimp, it is critical to examine the relationship between estuarine-dependent organisms and the quality of edge habitat. In our simulation model, edge habitat acted as a bridge between the vegetation and open water; yet in the northern Gulf of Mexico, the interface between vegetation and water often acts as a barrier rather than a bridge. For example, many natural marshscapes are fragmented by dredged canals or pipelines (Tabberer et al. 1985). Elevated spoil banks often line these canals and prevent aquatic organisms from crossing the water–vegetation interface. Structural marsh management is a second anthropogenic factor that can reduce marsh access. This management practice involves enclosing a marsh with levees and installing water-control structures to manipulate the hydrology of the enclosed area. Only a few studies have investigated relationships between estuarine organisms and landscapes impacted by impenetrable borders (Rogers et al. 1994, Rozas and Reed 1994, Rozas and Minello 1999); the quality of habitat produced by different edge environments needs to be further explored.

The results of this study highlight the importance of preserving habitats with natural edge. Simulated brown shrimp survival was higher in habitats with high edge than in habitats with low edge. Preserving habitats with natural edge may benefit other fisheries because shrimp represent an estuarine-dependent life-history strategy that is common to many ecologically and commercially important species (e.g., blue crab, red drum). Many estuarine-dependent fish display density patterns similar to that of brown shrimp. The most common small estuarine fishes are found highly concentrated in marsh edges (Baltz et al. 1993). The marshscape patterns that

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[8] ⟨http://www.st.nmfs.gov/st1/commercial/⟩

influenced simulated shrimp survival may therefore also influence the survival of other estuarine-dependent species.

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